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Contextual Variation in the Alarm-Call Responses of Dwarf Mongooses (*Helogale parvula*)

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Abstract

Alarm calling is a widespread anti-predator behaviour, but it is not always a reliable indication of real danger. Individuals must decide when to respond to alarm calls as a function of the relative costs and benefits, but experiments investigating contextual influences are rare. We use playback experiments in conjunction with supplementary feeding and the presentation of direct predator cues to examine variation in receiver responses to alarm calls in a habituated population of wild dwarf mongooses (*Helogale parvula*). First, we investigated whether individuals adjust their response to alarm calls depending on their own satiation level and spatial position of the caller. Individuals were more likely to respond to alarm calls when they had received supplementary food, and hence could prioritise minimisation of predation risk over starvation. There was also increased responsiveness to alarm calls given by individuals from elevated positions compared to those on the ground; sentinels (raised guards) are more likely to detect potential predators than foragers, and alarm calls from elevated positions are probably perceived as more reliable. When individuals did respond, they were more likely to flee following an alarm call given from ground level; foragers are likely to detect predators in closer proximity than sentinels, requiring more urgent escape responses. Second, we examined how individuals combine social information provided by alarm calls with personal information relating to predator presence. Receiver responses to terrestrial and aerial alarm calls did not differ when they followed interaction with an olfactory predator cue compared to an olfactory control cue. Following interaction with a terrestrial predator cue, however, latency to non-vigilance was significantly longer after hearing an aerial alarm call than a terrestrial alarm call, potentially because of social information novelty. Our results provide experimental evidence that receivers respond flexibly to alarm calls depending on receiver, signaller and external factors.

Keywords: alarm calls, vocal communication, predation risk, social information, anti-predator behaviour, dwarf mongoose.

Introduction

Alarm calling, the production of specific vocalisations on detecting a potential predator, is a vital component of anti-predator behaviour in many taxa (Seyfarth et al. 1980; Hollén and Radford 2009; Zuberbühler 2009). But, not all alarms reliably indicate the presence of a predator; false alarms, arising from unintentional signaller mistakes through to active

deception, are relatively common (Cresswell et al. 2000; Flower et al. 2011; Magrath et al. 2015). As a result, receivers must decide whether to respond to alarm calls depending on the relative costs and benefits. There are clear, potentially fatal costs of not responding to a genuine alarm, so animals typically show a high level of responsiveness, employing a ‘better-safe-than-sorry’ strategy (Beauchamp 2010). However, responding unnecessarily incurs the energetic costs of fleeing (Beauchamp 2010) and opportunity costs of suspending important behaviours such as foraging (Cresswell et al. 2000), so there exists considerable variation in receiver responses. That variation can arise as a consequence of differences in receiver, signaller or external factors.

All animals face trade-offs, including the pivotal starvation–predation trade-off which is central to many behavioural decisions (McNamara and Houston 1986; Lima and Dill 1990). The starvation–predation trade-off exerts considerable influence on anti-predator behaviours; for example, food-deprived individuals decrease personal vigilance behaviour (Lima 1995). It therefore seems likely that receivers would also adjust their response to alarm calls depending on the relative risk of starvation and predation. Indeed, theoretical models predict that when the amount of energy required for survival is large, the optimal strategy is not always to respond to alarm signals but to maximise available foraging time (Proctor et al. 2001). This theory has received empirical support in other sensory modalities (Smith 1996; Tibbetts 2008), and juvenile willow tits (*Poecile montanus*), whose access to food is less predictable than that of adults, respond less to the playback of alarm calls when feeding than do adults (Rajala et al. 2012). However, to our knowledge, no field study has experimentally tested the effect of receiver satiation on response to vocal alarm signals.

Alarm calls represent an example of ‘social’ information; that is, information acquired from other individuals (Giraldeau et al. 2002; Danchin et al. 2004). While obtaining social information is comparatively quick and easy, there are inconsistencies in its quality (Giraldeau et al. 2002), and receivers should therefore regulate their use of social information according to its likely reliability (Blumstein et al. 2004; Dunlap et al. 2016). There have been a small number of experimental demonstrations that receivers alter their responses to alarm calls based on assessments of inherent signaller reliability (Hare and Atkins 2001; Blumstein et al. 2004). The spatial position of the alarm caller might also be expected to play a role. In a range of social species, individual group members act as sentinels, adopting a raised position to scan for danger (reviewed in Bednekoff 2015). In general, sentinels are more successful at detecting predators

than foraging groupmates and alarm call sooner, as their elevated position affords them a wider field of view and fewer visual obstructions (Rasa 1987; Ridley et al. 2010; Sommer 2012). As a result, individuals may perceive the alarm calls of sentinels to be more reliable than those given by foragers, but this possibility has received little experimental testing.

Predation risk fluctuates in relation to a number of social and ecological variables (Seyfarth et al. 1980; Lima and Dill 1990; Hilton et al. 1999; Stankowitz and Blumstein 2005; Hollén et al. 2011; Chmura et al. 2016), and individuals should take current risk estimates into consideration when balancing the relative costs and benefits of responding to alarm calls. For instance, when group size is small, predation risk generally increases (Hamilton 1971), and individuals should more often respond to alarm calls (Proctor et al. 2001). Perceived risk also increases with habitat density (Whittingham and Evans 2004; Embar et al. 2011), and receivers therefore increase their responsiveness to alarm calls as lines of sight become more interrupted (Enstam and Isbell 2004; Frechette et al. 2014). In addition, prior information about current predation risk can influence alarm-call responses. For example, surveillance calls given by sentinels are known to provide an indication of current risk levels (Bell et al. 2009; Kern and Radford 2014), and foragers are more likely to respond to alarm calls when preceding surveillance calls have indicated a higher risk (Bell et al. 2009). Direct predator cues (cues produced by predators themselves; Nersersian et al. 2012), including acoustic cues such as vocalisations, or olfactory cues such as urine and faeces, also alter perceived predation risk (Hauser and Wrangham 1990; Weldon 1990). In the presence of direct cues, individuals adjust various behaviours to minimise risk, such as decreasing their tendency to vocalise, increasing vigilance and avoiding use of certain habitat patches (reviewed in Apfelbach et al. 2005). Individuals detect predators more quickly and raise the alarm sooner following exposure to direct predator cues (Zöttl et al. 2012), but to our knowledge, any effect of direct predator cues on the response of receivers to alarm calls remains to be tested.

Here we investigate variation in receiver responses to conspecific alarm calls in a wild but habituated population of dwarf mongooses (*Helogale parvula*). Dwarf mongooses are cooperatively breeding carnivores living in groups of up to 30 individuals (Rasa 1977). The dominant pair monopolizes reproduction, with related and unrelated subordinates of both sexes helping to rear offspring (Rood 1980). Dwarf mongooses search for the majority of their prey by digging, and so are unable to forage and be fully vigilant simultaneously (Rasa 1989). They are at risk from a wide range of avian and terrestrial predators (Rasa 1986; Kern and Radford

2013). Individuals alert others to the presence of predators using different alarm calls, which indicate predator type (aerial and terrestrial), and typically elicit escape responses by groupmates (Beynon and Rasa 1989; Collier et al. in revision). When groups are foraging, sentinels providing acoustic information about danger and predation risk are often present (Kern and Radford 2013, 2014; Kern et al. 2016). Dwarf mongooses also obtain considerable information in general, and about predators specifically, from olfactory cues (Christensen et al. 2016; Morris-Drake et al. 2016).

We use a combination of field-based experimental manipulations to investigate whether receivers adjust alarm-call responses depending on context (i.e. various receiver, signaller and external factors). First, we combine a playback experiment with supplementary feeding to examine whether foragers differ in their alarm-call responses depending on their own satiation level and the spatial position (height) of the caller. We expect receivers to increase responsiveness when they have received supplementary food, and thus can prioritise minimisation of predation over starvation, and when alarm calls are given by elevated individuals (sentinels) with better visibility over their surroundings than that of foragers. Second, we use playback of aerial and terrestrial alarm calls in conjunction with presentation of a direct terrestrial predator cue (urine) to investigate whether individuals combine personal and social information to adjust response thresholds. We expect receivers to increase responsiveness to terrestrial alarm calls when prior information from olfactory cues has suggested the presence of a terrestrial predator nearby.

Material and Methods

Study site and population

We studied a wild population of dwarf mongooses at Sorabi Rock Lodge Reserve, Limpopo Province, South Africa (24°11'S, 30°46'E) (see Kern and Radford 2013 for details). Data were collected from nine groups (mean group size = 6; range = 3–9), habituated to close observation (<5 m) on foot and generally visited every 3–4 days (Kern and Radford 2013, 2014). Animals are individually identifiable by blonde dye markings (Wella UK Ltd., Surrey, UK) on their fur, applied with an elongated paintbrush, or from natural features such as scars or facial irregularities. Since the population has been monitored continuously from 2011, the age of most individuals is known; individuals can be sexed through observations of ano-genital grooming (Kern et al. 2016). Adult group members were classified as either 'dominant' (male

and female pair) or ‘subordinate’ (the remaining individuals), as in previous work (Kern and Radford 2013, 2014; Kern et al. 2016). The dominant pair could be identified through observations of aggression, feeding displacement, scent marking and greeting behavior (Rasa 1977). All work was conducted under permission from the Limpopo Department of Economic Development, Environment and Tourism (permit number: 001-CPM403-00013), the Ethical Review Group of the University of Bristol, UK, and the Ethical Committee of Pretoria University, South Africa.

Acoustic recordings

All recordings were made at a sampling rate of 44.1 kHz with a 16-bit resolution onto a SanDisk SD card (SanDisk, Milipitas, California, USA), using a Marantz PMD660 professional solid-state recorder (Marantz America, Mahwah, NJ, USA) and a handheld highly directional Sennheiser ME66 shotgun microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK) with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK). Aerial alarm calls given to flying raptors (Fig. 1a) and close calls given continuously during foraging bouts (Fig. 1b) were recorded opportunistically from a distance of 0.5–10 m during behavioural observations. Terrestrial alarm calls given to predators on the ground (Fig. 1c) were recorded from a distance of 3–10 m during presentations of a domestic dog to groups (Collier et al. in revision). Ambient sound was recorded from approximately the centre of the territory of the focal group at similar times of day for all territories. To allow standardisation of playback amplitudes (see below), a HandyMAN TEK1345 Mini Sound Level Meter (Metrel UK Ltd., Normanton, West Yorkshire, UK) was used to measure the peak amplitude of naturally occurring sound levels (ambient sound: 40 dB sound pressure level A (SPLA) at 1 m; close calls: 55 dB SPLA at 1 m; alarm calls: 55 dB SPLA at 2 m).

Experiment 1

To assess the influence of receiver satiation and caller spatial position on responses to alarm calls, focal individuals (18 subordinate adults in seven groups) were exposed to four treatments between July and September 2014. Treatments consisted of combinations of two supplementary-feeding conditions (fed, unfed) and the playback of an alarm call from two caller positions (sentinel, forager). The four treatments took place on different days, separated

by a mean \pm SE 1.4 ± 0.1 days (range = 1–6 days), and were presented in a counterbalanced order.

When supplementary fed, focal individuals were given a quarter of a hard-boiled egg, out of sight of the rest of the group to avoid food theft. Supplementary feeding took place within 1 h of a group leaving their overnight refuge to minimise the effect of natural foraging on individual satiation state. Alarm-call playback took place as soon as possible after supplementary feeding (5–30 min), given the conditions required by the experimental protocol, or an equivalent time after leaving the refuge for no-feeding trials. Variation in the latency to playback after leaving the refuge did not significantly affect alarm-call responses (see Results).

Alarm-call tracks were constructed using Raven Pro (version 1.5, The Cornell Laboratory of Ornithology, NY, USA) and consisted of a single aerial alarm call from an adult male group member, 5 s into a 10-s recording of ambient noise. Since there is some evidence of individual recognition in dwarf mongooses using contact calls (Sharpe et al. 2013), and since the alarm calls of another mongoose species (meerkats, *Suricata suricatta*) are known to include individually distinct characteristics (Schibler and Manser 2007), identity of the caller was controlled for by using the same alarm call for all four trials to each focal individual. Different alarm calls were used for each focal individual. Tracks did not include any other mongoose vocalisations. Vocalisations were broadcast from an mp3 player (Apple Inc., Cupertino, California, USA) connected to a single portable speaker (Excel Audio, Guangzhou, China) positioned 2–5 m from the focal forager. ‘Sentinel’ alarm calls were broadcast from a height of 1.5 m to mimic the elevated position of a sentinel, and ‘forager’ alarm calls were broadcast from ground level. Playback amplitude was standardised according to the amplitude of naturally occurring aerial alarm calls (see above). Alarm calls were played when the entire group was foraging in the same habitat type under calm weather conditions. Playbacks took place when there had been no natural sentinel present for at least 5 min and no natural alarm call for at least 10 min. Following any major disturbances, such as an inter-group encounter or mobbing event, a minimum of 15 min elapsed before playback. Following the playback of each alarm call, the response of the focal individual (no response, freeze and be vigilant, or flee to cover) was noted, alongside latency to resume non-vigilant behaviour (e.g. movement, grooming, latrining).

Experiment 2

To assess the influence of direct predator cues on responses to alarm calls, each focal individual (nine subordinate adults from six groups) was exposed to four treatments between May and September 2015. Treatments consisted of combinations of two cue presentations (terrestrial predator cue, control cue) and two call playbacks (aerial alarm call, terrestrial alarm call). The four treatments took place on different days and were presented in a counterbalanced order. When order dictated that two predator cues be presented consecutively, a minimum of 48 h elapsed between treatments, otherwise treatments sometimes took place on consecutive days (mean \pm SE treatment separation = 4.3 ± 0.7 days; range = 1–15 days). To maximise the chances of focal individuals encountering the presented cues, trials were conducted at sleeping burrows; cue presentation during group foraging was deemed logistically unfeasible. All trials were conducted under calm weather conditions and at the same type of sleeping burrow (termite mounds), once all group members had emerged and before a group left to begin foraging.

As a predator cue, river sand soaked in cat urine was used. Cat urine and faeces have been used successfully as a predator cue in other mongoose research, including in our study population of dwarf mongooses (Zöttl et al. 2012; Morris-Drake et al. 2016). Urine-soaked sand was collected weekly from a litter tray used by a half-domestic half-wild cat and stored in an airtight plastic container until presentation (latency until use = 1–14 days). As a control cue, sand collected from the same river bed was presented. In all treatments, 1 cup of relevant sand was placed at the overnight refuge before any individuals had emerged; 1 tablespoon of water was poured on to the sand to ensure that both stimuli were similarly damp. Before the first mongoose emerged in the morning, the sand was placed 30 cm from the latrine site at the burrow (previously determined as part of the long-term project; see Christensen et al. 2016).

Once the focal individual had approached to within 10 cm of the sand, the aim was to start the alarm-call playback after 1 min. The size and shape of sleeping burrows meant that individuals sometimes moved out of sight of the observer, and playback was delayed until the focal individual was once again visible (mean latency to playback \pm SE = 101 ± 11 s, range = 60–300 s). This variation in timings did not significantly influence alarm-call responses (see Results). Alarm-call tracks were constructed using Raven Pro 1.5 and consisted of a single alarm call, 5 s into a 10-s recording of ambient noise. The same alarm call was used for the two trials of the same type (aerial or terrestrial) to the same focal individual, but different alarm-

call exemplars were used for each focal individual. Since the identity of alarm callers was often unknown for terrestrial alarm calls (Collier et al. in revision), all alarm calls used were from individuals in different groups to the focal individual to ensure that the latter were not being played their own vocalisations. Playback tracks did not include any other mongoose vocalisations.

Vocalisations were broadcast from an mp3 player (Apple Inc., Cupertino, California, USA) connected to a single SME-AFS portable field speaker (Saul Mineroff Electronics Inc., New York, USA), positioned on the ground 3 m from the cue facing away from the refuge. Playback amplitude was standardised according to the amplitude of naturally occurring alarm calls (see above). When a natural alarm call occurred before the focal individual interacted with the sand, or between interaction with the sand and the start of playback, or the focal individual left the sleeping burrow without interacting with the cue, the trial was abandoned and repeated on another day ($N = 9$). Sand was removed at the end of a trial once the group had left to forage.

Focal individuals were filmed using a handheld digital camera (Panasonic, Osaka, Japan, and Canon Inc., Tokyo, Japan). Recording began at the start of the interaction with the sand (predator or control cue) and continued until the individual had resumed non-vigilant behaviour following alarm-call playback. The following data were extracted from the videos using Quicktime Player 7.7.9 (Apple Inc., California, USA): total number and duration of vigilance scans in the 1-min period immediately after interacting with the sand; response to alarm call (no response, freeze and be vigilant, or flee to cover); and the latency to resume non-vigilant behaviour (e.g. movement, grooming, latrining).

Statistical analyses

All analyses were performed using R version 3.2.4. All tests were two-tailed and were considered significant at $P < 0.05$. Parametric tests were conducted where data fitted the relevant assumptions of normality and homogeneity of variance. Transformations were conducted to achieve normality of errors in some cases (details below), otherwise non-parametric tests were used.

Data were analysed using linear mixed models (LMMs) and generalized linear mixed models (GLMMs), to take account of repeated measures from the same individual and group. All likely

explanatory terms were included in the maximal model. Model simplification was then conducted using stepwise backward elimination (Crawley 2005), with terms sequentially removed by order of least significance and models compared using likelihood ratio tests. Removed terms were returned to the minimal model individually to confirm that they were not significant. Presented χ^2 and *P*-values for significant terms were obtained by comparing the minimal model with models in which the term of interest had been removed. Presented χ^2 and *P*-values for non-significant terms were obtained by comparing the minimal model with models in which the term of interest had been added. Presented effect sizes (\pm SE) were obtained from the minimal model. Random-effects models with a common subject slope but different intercepts were used, since observations were not replicated (Barr et al. 2013). For categorical terms, differences in average effects are shown relative to one level of the factor, set to zero. Analyses were carried out using the lme4 or glmmADMB packages when data were zero-inflated (Fournier et al. 2012). The specific nature of independent and dependent variables as well as the statistical technique used to address each of the main questions are outlined below.

To examine immediate response to alarm calls in Experiment 1, two binomial GLMMs were run. The first investigated whether individuals responded (no response = 0, freeze and be vigilant or flee to cover = 1), the second investigated the type of response shown by those individuals that did respond (freeze and be vigilant = 0, flee to cover = 1). To examine latency to resume non-vigilant behaviour, a LMM was used following log-10+1 transformation of the data. For all models, the fixed effects of supplementary-feeding condition (fed or unfed), alarm-caller position (forager or sentinel), trial order (1–4), latency to alarm-call playback, and the interaction between supplementary-feeding condition and alarm-caller position were fitted, and focal individual nested in group was included as a random term.

To establish whether mongooses responded to presentation of the predator cue compared to the control cue in Experiment 2, two LMMs were used to analyse total number and total duration of vigilance scans (both following square-root transformation) in the 1-min period immediately after interaction with the cue. In 6 trials, the focal individual moved out of sight during the 1-min period immediately after interacting with the sand, thus vigilance measures were only available for 30 trials. To examine response type to the alarm-call playback by those individuals that responded (35 out of 36 trials where the focal individual was visible; no statistical analysis was therefore undertaken on whether individuals responded), a binomial GLMM was conducted (freeze and be vigilant = 0, flee to cover = 1). To examine latency to resume non-

vigilant behaviour, a LMM was used following log-10+1 transformation of the data. For all models, the fixed effects of cue type (predator or control), alarm-call type (aerial or terrestrial), trial order (1–4), latency to alarm-call playback and the interaction between cue type and alarm-call type were fitted, and focal individual nested in group was included as a random term.

Results

Experiment 1

Individuals that had been supplementary fed were significantly more likely to respond (by fleeing or becoming vigilant) to an alarm call than those that had not been fed (Table 1a, Fig. 2a). Examining only those cases when an individual responded to an alarm call, there was no significant effect of supplementary-feeding treatment on response type (Table 1b). Latency to resume non-vigilant behaviour was not significantly influenced by whether the forager had received supplementary food (Table 1c).

Individuals were significantly more likely to respond when the alarm call was broadcast from a height of 1.5 m (as if from a sentinel) compared to ground level (as if from a forager) (Table 1a, Fig. 2b). Examining only those cases when an individual responded to an alarm call, individuals were significantly more likely to flee (rather than become vigilant) following an alarm call originating from a ‘forager’ compared to a ‘sentinel’ (Table 1b, Fig. 2c). Latency to resume non-vigilant behaviour was not significantly influenced by alarm-caller position (Table 1c).

Experiment 2

Foragers were significantly more vigilant in the 1-min period immediately after encountering a direct predator cue than a control cue (total number of vigilance scans: Table 2a, Fig. 3a; total duration of vigilance scans: Table 2b, Fig. 3b). Examining the 35 cases when an individual responded to an alarm call, the likelihood of fleeing (as opposed to becoming vigilant) was not significantly influenced by prior exposure to direct predator cues (Table 3a). However, latency to return to non-vigilant behaviour was significantly influenced by the interaction between alarm-call type and cue type (Table 3b). Following playback of a terrestrial alarm call, latency to become non-vigilant was not significantly affected by presence or absence of direct predator cues, but following playback of an aerial alarm call, latency to become non-vigilant was significantly greater in the aftermath of interaction with a direct predator cue compared to the control treatment (Fig. 4).

Discussion

Dwarf mongooses responded differently to conspecific alarm calls depending on receiver satiation, signaller spatial position and prior information about current predation risk. Our work therefore provides rare experimental evidence for context-dependent responses to alarm calling.

Receiver satiation

As predicted, foragers were more likely to respond to alarm calls when they had received supplementary food; this finding provides empirical support for the theoretical modelling of Proctor et al. (2001). When faced with behavioural decisions about the need for anti-predator behaviours, foraging animals are subject to the trade-off between starvation and predation (McNamara and Houston 1986; Lima and Dill 1990). Supplementary feeding decreases the amount of energy that individuals need to acquire, thus the risk of predation is likely to outweigh the risk of starvation and individuals can afford to err on the side of caution with respect to alarm calls. Supplementary feeding did not, however, change the type of response; there was no increase in the likelihood of a flee response compared to vigilance behaviour. It is possible that the quantity of supplemental food provided was insufficient, and individuals would be more likely to flee were more provided.

Signaller height

As predicted, foraging dwarf mongooses adjusted their response to alarm calls depending on the height of the caller. They responded more often to an alarm call when it was broadcast from a high position, mimicking a sentinel, compared to at ground level, mimicking a forager. This result supports work on pied babblers showing that foragers decrease their vigilance and gain an increase in biomass intake in response to surveillance calls from sentinels in a higher position (Radford et al. 2009). Whether and how animals make use of social information depends on its perceived quality, which can depend on the reliability of the caller (Hare and Atkins 2001; Danchin et al. 2004). Sentinels, in their elevated position, benefit from a wider field of view and reduced visual obstructions compared to foragers, and are thus more likely to detect potential predators; they are often the first group members to give an alarm call to approaching danger (Rasa 1987; Ridley et al. 2010; Sommer 2012). Sentinel alarm calls may therefore be perceived as a more reliable indicator of danger than alarm calls by foragers, and should not be ignored.

Examining only cases when receivers responded, individuals were more likely to flee than become vigilant in response to an alarm call by a ‘forager’ compared to a ‘sentinel’. Elevated callers may not only be better at detecting predators in general, but may also be able to detect them at a greater distance. For instance, in Arabian babblers (*Turdoides squamiceps*), sentinels begin alarm calling sooner and predominately produce the type of alarm call given to distant predators, whereas foragers produce more of the call type specifying closer threats (Sommer 2012). In general, alarm calls given by foragers may therefore be perceived as more urgent than those of sentinels, and receivers should respond more strongly to maximise their chances of survival (Proctor et al. 2001; Sieving et al. 2010). When alarm calls are given in less urgent contexts, in this case by sentinels, the optimal receiver response may be to delay fleeing, allowing for personal assessment of the threat and avoiding an unnecessary escape response (Quinn and Cresswell 2005). Fleeing is costlier than vigilance, entailing additional energetic costs above those associated with the interruption of foraging, and has the potential to cause fatal errors, including escaping in the wrong direction (Shifferman and Eilam 2004) or in a manner inappropriate to the specific predator (Cresswell 1993), and miscalculating the path and speed of the approaching threat (Kullberg et al. 1998; Lind et al. 2002).

Current predation risk

As predicted, our second experiment found that exposure to direct predator cues increased perceived risk level, with foragers demonstrating heightened vigilance after interacting with a predator cue compared to a control cue; this response has been found in a variety of species, including our mongoose population (Apfelbach et al. 2005; Morris-Drake et al. 2016). Despite this perceived increase in risk, dwarf mongooses were no more likely to flee in response to a subsequent alarm call than when they had interacted with a control cue. It is possible that the increase in vigilance following interaction with the predator cue effectively cancelled out the increased risk; having personally sampled the environment, individuals responded to alarm calls as they typically would. This appears to contradict the ‘flush early and avoid the rush’ hypothesis, which predicts an increase in responsiveness after greater vigilance, with individuals taking flight sooner on detection of a potential predator (Blumstein 2010; Samia et al. 2013; Shannon et al. 2016). This hypothesis deals with visual detection of predators by individuals themselves, however, and may not hold true for use of social information such as alarm calls. Another possibility is that the low variation in receiver response stems from the

fact that, to maximise the likelihood that predator and control cues were encountered by focal individuals, the experiments took place at sleeping refuges. Perceived risk typically reduces with decreasing distance from refugia (Camp et al. 2012), thus individuals may have viewed all situations as relatively low risk given their immediate proximity to a refuge. It is worth noting, however, that predator olfactory cues resulted in increased vigilance, and 35 of 36 alarm calls led to either vigilance or fleeing; the mongooses are still acting as though there is some level of danger even when close to a refuge. A different relationship between pre-exposure to olfactory predator cues and subsequent alarm-call responses may be found when individuals are further away from a refuge or in an unfamiliar area; such variation would also constitute a context-dependent response to alarm calls, and could be examined in future work.

Receivers took longer to resume non-vigilant behaviour after responding to an aerial alarm call that had been preceded with a terrestrial predator cue than in any other treatment combination. This contradicts our expectation that a terrestrial alarm call following interaction with a terrestrial predator cue, where social information supported recently gathered personal information, would be perceived as most threatening. It is possible that aerial alarm calls may always be perceived as riskier, since animals often perceive aerial predators as more threatening (Lima 1993). This seems unlikely in our experiment, however, as following exposure to a control cue, latency to non-vigilance was no longer following an aerial compared to a terrestrial alarm call. To aid decision-making processes, individuals combine personal and social information flexibly depending on their relative availability and reliability (van Bergen et al. 2004; Rieucou and Giraldeau 2011). Individuals showed greater personal vigilance after interaction with a predator cue, probably inspecting the environment for terrestrial predators specifically (Zöttl et al. 2012), rather than potential predators in general. Having gathered personal information, individuals may have satisfied themselves of the risks posed by terrestrial predators, thus the information provided by terrestrial alarm calls may effectively be redundant. Individuals may have remained uncertain of the threat from aerial predators, however, and the heightened response to aerial alarm calls, which offer novel information to the receiver, may in fact be the optimal strategy.

Conclusions

In conclusion, we show that dwarf mongoose receivers exhibit considerable contextual flexibility in their responsiveness to alarm calls. Our results support previous findings that the

use of social information depends on signal quality (Hare and Atkins 2001; Blumstein et al. 2004; Radford et al. 2009), as well as highlighting the role of social information novelty when combining personal and social information. Our study also suggests that, as predicted by theoretical models (Proctor et al. 2001), responses to alarm calls are strongly influenced by the starvation–predation trade-off. To understand further the trade-offs involved in alarm-call responses, future research should investigate variation in the costs of response depending on response intensity.

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Figures

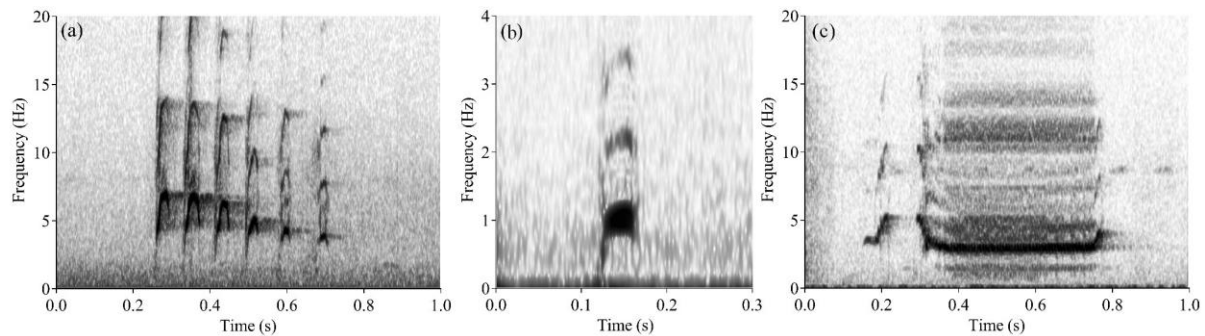


Figure 1. Illustrative spectrograms of dwarf mongoose vocalisations used in playback experiments: a) aerial alarm call, (b) close call and (c) terrestrial alarm call. Spectrograms were created using Raven Pro 1.5 (FFT length 1024, Hann window, 75% overlap, 1.45 ms time resolution, 43 Hz frequency resolution).

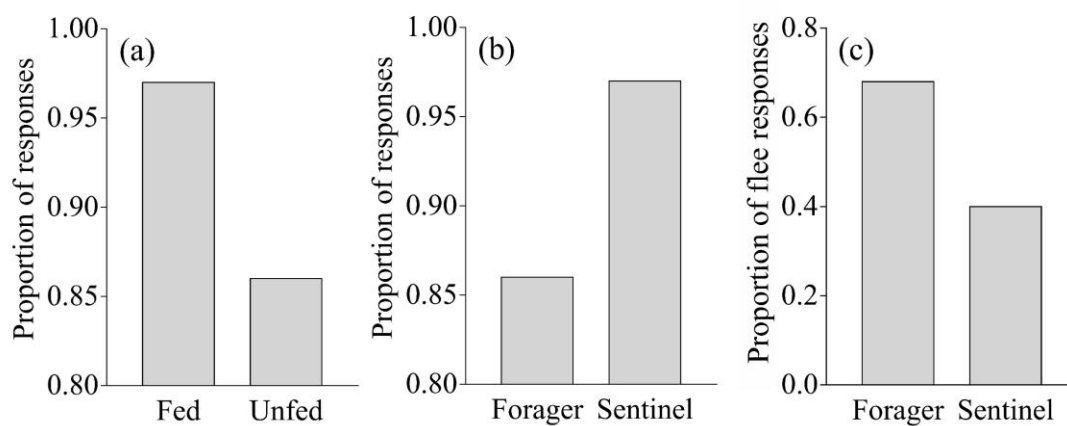


Figure 2. Responses of dwarf mongooses to playback of aerial alarm calls. Likelihood of responding (fleeing or becoming vigilant) rather than continuing foraging depending on (a) whether focal individuals were supplementary fed and (b) whether the alarm call was played back from 1.5 m height (sentinel) or ground level (forager). (c) Likelihood of fleeing (rather than becoming vigilant) depending on whether the alarm call was played back from 1.5 m height (sentinel) or ground level (forager). $N = 72$ trials, 18 individuals, seven groups.

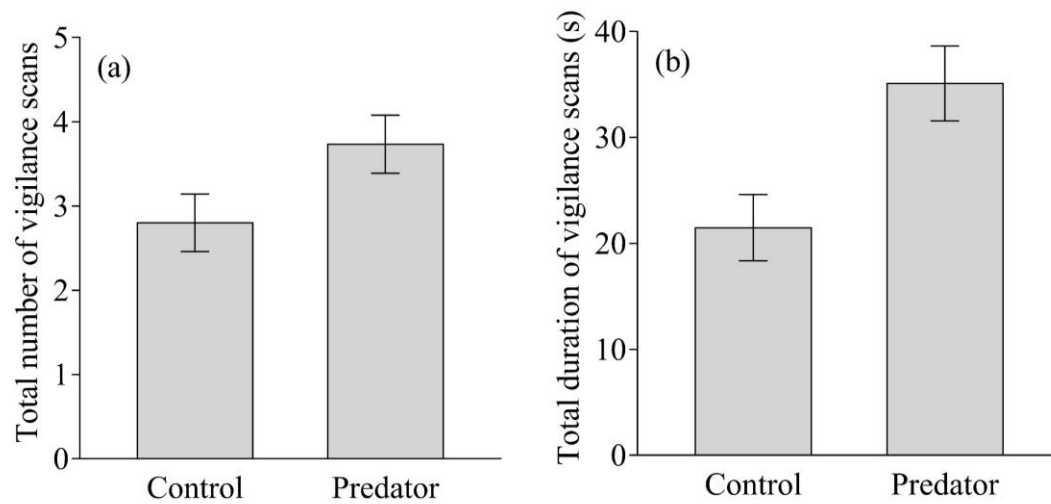


Figure 3. Responses of dwarf mongooses to the presentation of a direct predator cue or control cue. Shown are mean and SE (a) total number of vigilance scans and (b) total duration of vigilance scans calculated from the raw data. $N = 30$ trials, 10 individuals, six groups.

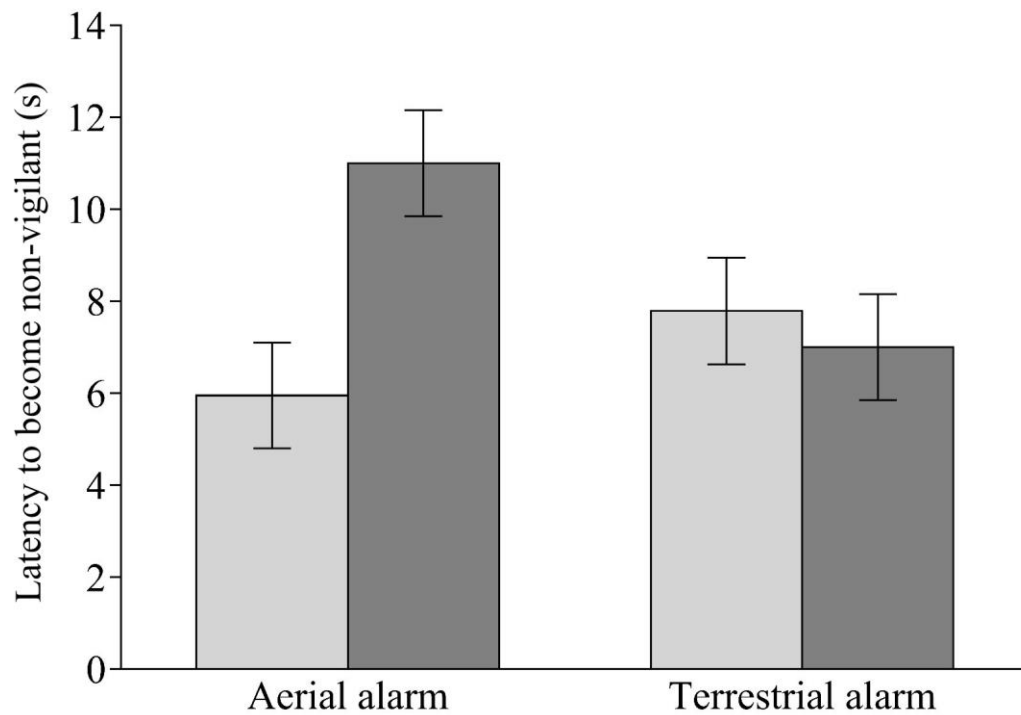


Figure 4. Latency to return to non-vigilant behaviour after playback of aerial or terrestrial alarm calls depending on prior interaction with either a control cue (pale grey bars) or a direct predator cue (dark grey bars). Means and standard errors were plotted using back-transformed means predicted from a GLMM (Table 3). $N = 35$ trials, nine individuals, six groups.

Tables

Table 1. Output from mixed models investigating the influence of supplementary-feeding condition and alarm-caller position on (a) likelihood of response (GLMM), (b) response type (GLMM), and (c) latency to return to non-vigilant behaviour (LMM) ($N = 72$ trials, 18 individuals, seven groups). Significant fixed terms shown in bold; variance \pm SE reported for random terms.

	Fixed effect	Effect \pm SE	df	χ^2	P
(a) Response					
Minimal model	(Intercept)	18.62 \pm 6.92			
	Alarm-caller position		1	9.42	0.002
	Forager	0.00 \pm 0.00			
	Sentinel	9.63 \pm 4.91			
	Supplementary feeding		1	9.42	0.002
	Fed	0.00 \pm 0.00			
Dropped terms	Unfed	-9.63 \pm 4.90			
	Latency to playback		1	0.81	0.370
	Trial order		3	0.41	0.938
	Supplementary feeding*Alarm-caller position		1	0.00	0.989
Random terms	Group	0.00 \pm 0.00			
	Individual ID nested in group	312.40 \pm 17.67			
(b) Response type					
Minimal model	(Intercept)	0.40 \pm 0.65			
	Alarm-caller position		1	4.63	0.031
	Forager	0.00 \pm 0.00			
	Sentinel	-1.31 \pm 0.64			
Dropped terms	Supplementary feeding		1	2.90	0.088
	Trial order		3	2.07	0.558
	Latency to playback		1	0.27	0.610
	Supplementary feeding*Alarm-caller position		1	0.01	0.918
Random terms	Group	0.43 \pm 0.65			
	Individual ID nested in group	0.00 \pm 0.00			
(c) Latency to non-vigilant behaviour					
Minimal model	(Intercept)	1.07 \pm 0.10			
Dropped terms	Trial order		3	6.05	0.109
	Latency to playback		1	1.99	0.158
	Supplementary feeding		1	0.32	0.570
	Supplementary feeding*Alarm-caller position		1	1.36	0.715
	Alarm-caller position		1	0.03	0.859
Random terms	Group	0.04 \pm 0.20			
	Individual ID nested in group	0.02 \pm 0.15			

Table 2. Output from two LMMs investigating focal vigilance in the 1-min period immediately after interaction with a direct predator cue or control cue: (a) total number of scans (square-root transformed), and (b) total duration of scans (square-root transformed) ($N = 30$ trials, 10 individuals, six groups). Significant fixed terms shown in bold; variance \pm SE reported for random terms.

	Fixed effect	Effect \pm SE	<i>df</i>	χ^2	<i>P</i>
(a) Total number of scans					
Minimal model	(Intercept)	1.90 \pm 0.09	1	4.16	0.041
	Cue type				
	Control	0.00 \pm 0.00			
	Predator	0.27 \pm 0.13			
Dropped terms	Trial order		3	4.75	0.191
Random terms	Group	0.00 \pm 0.00			
	Individual in group	0.00 \pm 0.00			
(b) Total duration of scans					
Minimal model	(Intercept)	5.87 \pm 0.36	1	8.31	0.004
	Cue type				
	Control	0.00 \pm 0.00			
	Predator	2.17 \pm 0.37			
Dropped terms	Trial order		3	6.33	0.097
Random terms	Group	0.00 \pm 0.00			
	Individual in group	0.28 \pm 0.53			

Table 3. Output from mixed models investigating (a) response type (GLMM), and (b) latency to non-vigilant behaviour (LMM) in response to aerial and terrestrial alarm-call playback following interaction with a direct predator cue or control cue ($N = 35$ trials, nine individuals, six groups). Significant fixed terms shown in bold; variance \pm SE reported for random terms.

	Fixed effect	Effect \pm SE	<i>df</i>	χ^2	<i>P</i>
(a) Response type					
Minimal model	(Intercept)	0.62 ± 0.48			
Dropped terms	Trial order		1	1.14	0.285
	Cue type		1	0.89	0.346
	Alarm-call type		1	0.28	0.595
	Cue type*Alarm-call type		3	1.46	0.689
	Latency to playback		1	0.00	0.945
Random terms	Group	0.43 ± 0.65			
	Individual ID nested in group	0.00 ± 0.00			
(b) Latency to non-vigilant behaviour					
Minimal model	(Intercept)	0.77 ± 0.06			
	Cue type*Alarm-call type		3	8.08	0.004
	Predator:Terrestrial	-0.30 ± 0.10			
	Alarm-call type				
	Aerial	0.00 ± 0.00			
	Terrestrial	0.12 ± 0.07			
	Cue type				
Dropped terms	Control	0.00 ± 0.00			
	Predator	0.30 ± 0.70			
	Trial order		3	0.95	0.330
Random terms	Latency to playback		1	0.08	0.770
	Group	0.01 ± 0.09			
	Individual ID nested in group	0.00 ± 0.00			